THE AUXO-THERMAL INTEGRATION OF CLIMATIC COMPLEXES[1]

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Some features of the life of a plant depend so largely upon a simple and uncomplicated enzymatic action, oxidation or other form of energy release, reduction, absorption or hydratation that their course may run parallel to that of a reaction the velocity of which is known and expressible by exponential law. As examples of this may be cited the development of buds or the germination of seeds in which the hydrolysis of accumulated food-material and the measurable development ensue at a rate in accordance with van't Hof's rule by which the velocity increases two or three times with every rise of temperature of 18° F.[2]

Many of the more important activities of living matter, however, are the combined expression of a complicated group of reactions, in which the initiating temperature, and the acceleration above it are not identical or parallel, and these may be linked with still others which are not a function of temperature.

It follows therefore that the resultant may be one not calculable from known data concerning reaction velocities. This is true of growth, differentiation and of the constructive processes in general, both in a morphogenic and physiologic sense.

It is obvious that if we are to make any rational interpretation of the entire effect of temperature upon the organism in any phase of its activity, or during all of its ontogeny a method must be formulated by which the effect of the duration and intensity of the temperature exposure upon the organism may be calculated. Now since this may not be done in terms of the reaction velocity of any of the underlying or component chemico-physical activities our only recourse is to use a resultant standard, one derived from the organism itself. In other

[1] Paper read in the Symposium on "Temperature Effects" before the Botanical Society of America at Atlanta, December 31, 1913.

[2] See Drinkard, Fruit-bud Formation and Development. Ann. Rep. Va. Polytech. Inst. Agr. Exper. Sta. 206–212, 1909 and 1910, as an example of the application of physio-chemical constants to developmental processes.

words, it is proposed to measure climate in terms of protoplasmic activity, a procedure that has become necessary in the experimental tests of the effect of climatic complexes upon plants now being carried out at the Desert and Coastal Laboratories and the attached plantations. If any rational analysis is to be made of the direct and inheritable effects that have come under observation in this work it must be done upon the basis of determinations of the influence of the separate environic components, of which of course temperature is one of the most important.

The author's work led him to a realization of the necessity for such a method in 1900 and the first attempts at anything definite were presented at the Denver meeting of the A. A. A. S. in 1901. The method then proposed consisted simply in estimating the area of the thermographic diagram by the line of freezing point and by the temperature tracing from the beginning of a season until a plant had attained a certain stage of its development. The vertical component in such figures being degrees of temperature, and the horizontal element being elapsed time, the resulting amounts were designated as *hour-degrees*. Thus the silver maple (*Acer saccharinum*) was found to have been exposed to 3,466 hour-degree units from the winter solstice until the time of blooming on March 26, 1901. *Draba verna* reached a similar state in 974 hours after an exposure of 1,644 units of exposure.[3]

This method was superior to all previous methods of summation of temperature-effects in that it gave full value to the time factor of exposure, which the older methods of cumulation, or of totalizing maxima or averages of daily temperatures did not. It was obviously a purely empirical procedure, as growth at all temperatures above the freezing was taken as uniform. The use of the freezing point as a physiological zero has much in its favor in phenological observations such as those upon Acer and Draba noted above, but a method of wider usefulness would assume a zero above this point.

As applied to the possibilities of growth it gave a value for the year of 78,836 hour-degree units to a meadow in the New York Botanical Garden and to the floor of the hemlock forest within four hundred yards of 68,596 units, a basis of comparison generally in harmony

[3] MacDougal, D. T. The temperature of the soil. Jour. N. Y. Bot. Garden **3**: 125. 1902, and Factors affecting the seasonal activities of plants. Plant World **10**: 218. 1907.

with the results of observations upon temperature and growth in the two places.[4]

Livingston has recently used a modified summation method dealing with temperature effects in phytogeography by which the mean normal temperatures are evaluated in terms of a reaction velocity assumed to be doubled for every rise of 18° F.,[5] and the results correlated with the occurrence of dominant types of vegetation in America. Distribution however, is, so far as temperatures are concerned, a function of growth or development possibilities and of endurance of maxima and minima as has been pointed out by Dr. Shreve. This method is then also to be classed as an empirical procedure since the rate of growth of a plant through its temperature range is not to be expressed in a single formula, and the rate during part of the tonic range is much greater than that assumed. Thus the temperature coefficient of growth of *Lupinus albus* is 3.7 between 14.4 and 24.2° C, 4.9 between 17 and 26° C., while that of *Zea mais* is 5.3 between 24.2 and 29° C., and 6.4 between 23.5 and 33.5° C. The rate of growth of wheat (*Triticum vulgare*) between its minimum of 40° F. and 58° F. is 5, and the temperature coefficient from 58 to 76° F. is 11, as may be seen by reference to figure 1.

The first step in the selection of a standard by which the constructive processes of organisms might be measured consists in fixing upon some form of activity, which is delicately affected by temperature and is readily measurable. Growth-extension or expansion seems to meet these requirements most fully, and this selection has the additional advantage that a large number of measurements of the actual rate in several species are already available.

The graphs representing the rate of growth of the higher plants show that these in general begin with a *miminum* variously placed with respect to several species, that the rate runs through several degrees of temperature with but little increase, then at a certain point the acceleration with the rise in temperature is extremely rapid until an *optimum* is reached. If the temperature rises above this point growth and development decrease and rapidly decline to zero.

[4] MacDougal, D. T. The seasonal activities of plants; factors affecting distribution and development. Sc. Am. Suppl., October 17, p. 251, 1908.

[5] See Livingston, B. E. Temperature Coefficient in Plant Geography and Climatology, Bot. Gaz. **56**: 349–375, 1913. The titles of several papers relative to reaction velocity in organisms are cited by this author.

These critical points are so widely apart (as much as 25° F. in various species) that anything like a generalized expression of the course or rate of growth of the higher plants would have but little value as a standard for the derivation of a unit for measuring the biologic effects of climate. It was therefore determined that evaluation of temperature exposures must for the present be made in terms of the activity of some single plant, and it may well fall out later that the generalization from a group of species may be of greater value. Many reasons make the data obtained from the growth of monocotyledons more valuable for the purpose mentioned, and several series of measurements of the rate of growth of wheat made by Köppen, deVries and others being available, these were used for testing the method proposed for estimating the temperature factor in the climate of a place. It is to be noted however that these measurements were made on the roots, "hypocotyls" or other parts of young plants, for the most part under equable conditions and it may not be assumed that the illumination or humidity was in all cases under good control. The available data however show that growth elongation begins at about 40° F., rises very slowly in rate to about 63° F., then accelerates rapidly to 86.5° F. with however a break or check between 80° and 83° F. The rate of growth at the highest temperature given was found to be 105 mm. in 48 hours, but, above this, growth is checked and during a further rise of 11° the rate falls to 5.4 and comes to zero at 108° F. (see figure 1). The first check in the rate of growth above 80° F. seems to have been found in several species and the most rational suggestion is that it may be attributed to some change in phase of the colloids, perhaps of the suspensoids. The final comprehensive drop follows a course highly suggestive of the procedure in which invertases and other specific substances are destroyed by high temperatures or their action inhibited.

An extensive series of calibrations have already been begun at the Desert Laboratory and at the Coastal Laboratory in which the rate of growth of the internodes from the upper part of the stem will be measured in such manner as to give the possibility of some interpretation of both the temporary and final retardation of growth in terms of physico-chemical processes. The data already at hand may be used for the present, and if our measurements differ from them the new factors may be applied to the figures obtained from the thermograph sheets in place of those expressed in the graph shown in figure 1.

Assuming now that it is desired to evaluate the variable temperature of any place or of any experimental setting it is first of all necessary to secure a reliable thermograph record for the period under investigation which might include the entire frostless season or the time in which a certain stage of development of selected organisms had been accomplished. Next, this record is ruled by lines which will divide it into figures, the area of which, measured by a planimeter, represents the length of time applied to the intensity of the temperature. The obvious procedure is simply to construct regular figures which shall include the area of the thermographic diagram as nearly as possible and to make these figures of such size that the use of averaged rates of growth will include the smallest practicable error (see figure 2). Crude as this method may appear in this preliminary form it however deals with actual and observable facts and all of its essentials are capable of correction. The first step in such improvement would of course consist in the re-measurements noted above under conditions approximating the daily range with corrections for the age of the material and with control of all of the environic factors. It may be expected that growth of the upper part of the stem from material newly formed in the leaf-blades will be different from that which might take place in organs in direct connection with the relatively great stores of easily hydrolyzable material in the seeds.

In the case of the wheat plant it has been found most convenient in this preliminary essay to calibrate growth vlaues at the average rate between 40 and 65° F., 65° and 70°, 70° and 75°, 75° and 80°, 80° and 85°, 85° and 92° F., etc. The lowest rate, including a range of 25° F., the areas measured on the thermograph sheet, in every case should have a similar ideal range to avoid distortion of results.

The summation of the results of the use of the planimeter on the thermograph sheets gives the total hour-degrees during a week, month or any other period during which the temperature stood within the limits mentioned and it will then be but necessary to apply to this sum the factor expressing the rate of growth to obtain the relative value of the exposures as is illustrated by the tables below constructed from data obtained at the Desert and Coastal Laboratories.

COASTAL LABORATORY, 1912

January				
	40–65° F.	56.4 × 4.5	254.7	
		1.3 × 20.	26.0	280.7
February				
	40–65	70.8 × 4.5 (28 days)	307.8	
		Total for 29 days..........	318.0	318.0
March				
	40–65	76. × 4.5	342.0	
	65–70	3.4 × 20.	68.0	410.0
April				
	40–65	68.7 × 4.5	308.1	
		1. × 20.	20.	328.1
May				
	40–65	97.2 × 4.5	437.4	
	65–70	4. × 20.	80.	517.4
June				
	40–65	111.4 × 4.5	501.3	
	65–70	23.7 × 20.	474.0	
	70–75	5.0 × 45.	225.0	
	75–80	1.7 × 70.	119.0	
	80–85	1. × 78.	78.	1,379.3
		Total....................		3,233.5

COASTAL LABORATORY, 1913

January				
	40–65° F.	47. × 4.5	211.5	211.5
February				
	40–65	60. × 4.5	270.	
	65–70	1.5 × 20.	30.	300.0
March				
	40–65	62.3 × 4.5	280.4	
	65–70	9.7 × 20.	194.0	
	70–75	1.5 × 45.	67.5	541.9
April				
	40–65	79. × 4.5	355.	
	65–70	4.2 × 20.	84.	439.5
May				
	40–65	99.2 × 4.5	446.4	
	65–70	12.3 × 20.	246.0	692.4
June				
	40–65	103.7 × 4.5	466.7	
	65–70	15.6 × 20.	312.0	
	70–75	2.9 × 45.	131.5	
	75–80	1. × 70.	70.	980.2
		Total..................		3,165.5

Desert Laboratory, 1912

January				
	40–65° F.	120.4 × 4.5 × .8	433.4	
	65–70	20.3 × 20. × .8	324.5	
	70–75	18.6 × 45. × .8	669.6	
	75–80	5.5 × 70. × .8	318.	
		Total		1,745.5
February[6]				
	40–65° F.	75.3 × 4.5 × .8	38.	309.
	65–70	15.8 × 20. × .8	36.1	288.9
	70–75	31.6 × 45. × .8	162.5	1,300.0
	75–80	2.1 × 70. × .8	16.8	134.4
		Total		2,032.3
March				
	40–65° F.	134.3 × 4.5 × .8	483.5	
	65–70	36.7 × 20. × .8	587.2	
	70–75	24.3 × 45. × .8	874.8	
	75–80	8.4 × 70. × .8	470.4	
		Total		2,415.9
April				
	40–65° F.	97.4 × 4.5 × .8	330.6	
	65–70	37.1 × 20. × .8	593.6	
	70–75	37.0 × 45. × .8	1,332.0	
	75–80	16.6 × 70. × .8	929.6	
	80–85	6.5 × 78. × .8	405.6	
	85–90	2.5 × 95. × .8	190.0	
		Total		3,781.4
		Total		9,974.0

Desert Laboratory, 1913

January				
	40–65° F.	87.7 × 4.5 × .8	315.7	
	65–70	21.9 × 20. × .8	350.4	
	70–75	17.1 × 45. × .8	615.6	
	75–80	1.4 × 70. × .8	78.4	
		Total		1,360.1
February				
	40–65° F.	106.9 × 4.5 × .8	384.8	
	65–70	19.6 × 20. × .8	313.6	
	70–75	14.9 × 45. × .8	536.4	
	75–80	5.7 × 70. × .8	319.2	
		Total		1,554.0

[6] The record of five days was missing and the month was taken at 28 days one-seventh being added to bring the amounts up for comparison with other years and other places.

Note: The areas of the sheets at the Desert Laboratory and the Coastal Laboratory are as 5 to 4 and hence data from the first-named place are to be multiplied by .8 to reduce to equivalent terms.

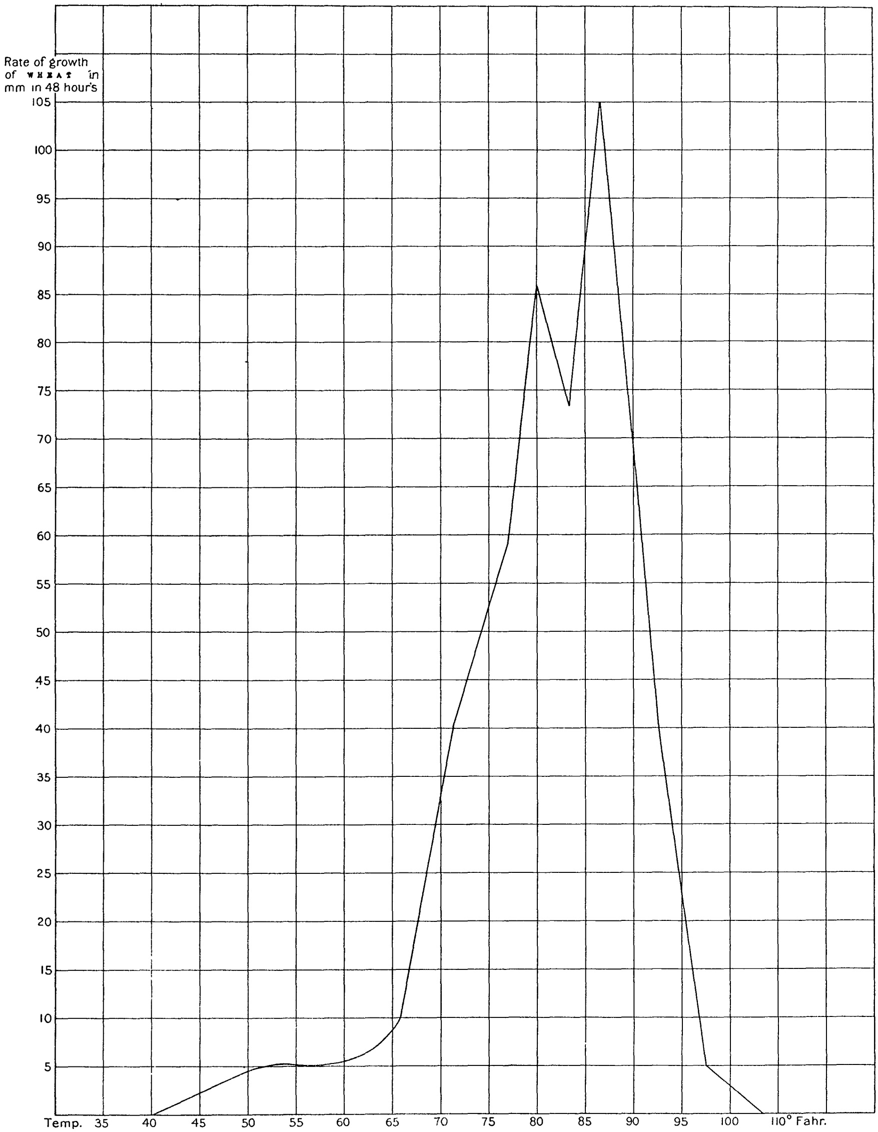

FIG. 1.

MACDOUGAL: CLIMATIC COMPLEXES.

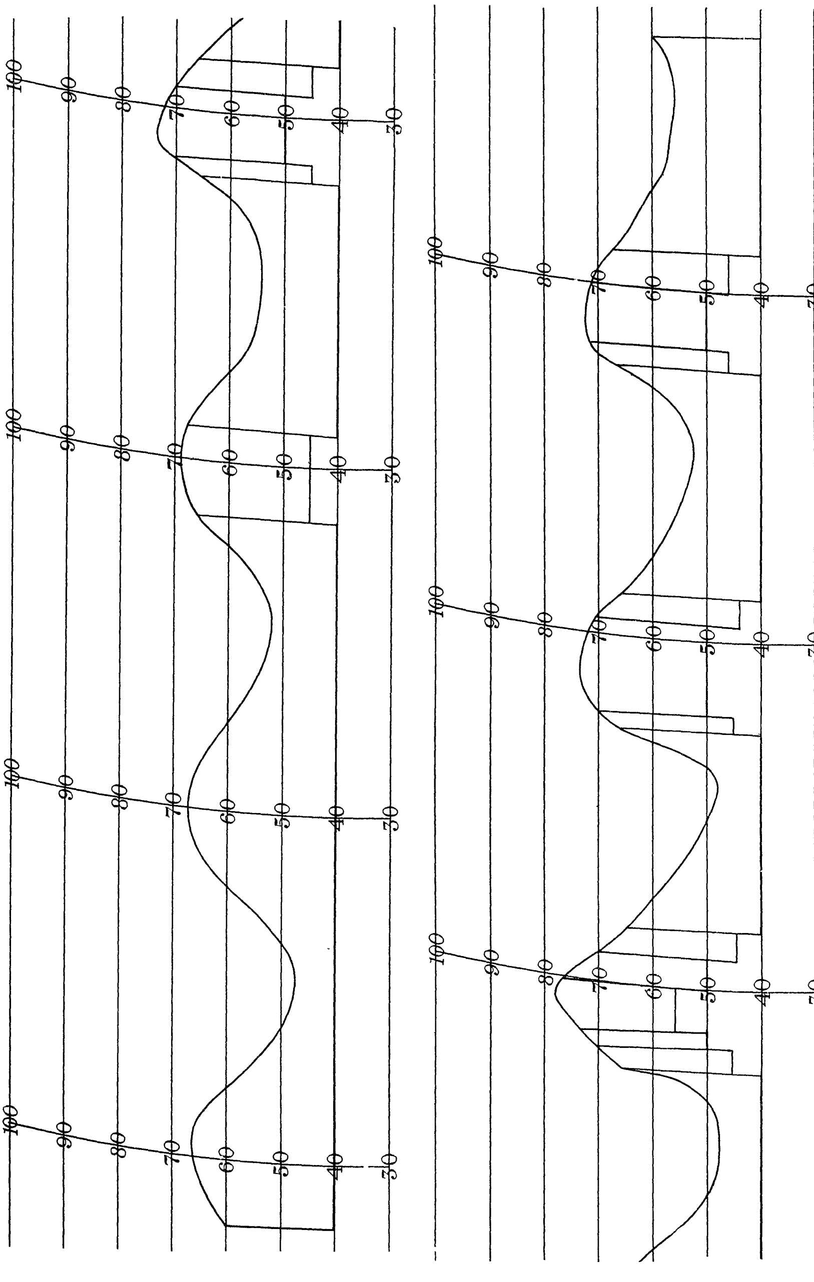

FIG. 2. Thermograph record, Coastal Laboratory, Carmel, California, June 16–23, 1913.

MACDOUGAL: CLIMATIC COMPLEXES.

March				
	40–65° F.	80.4 × 4.5 × .8	289.44	
	65–70	25.2 × 20. × .8	403.2	
	70–75	18.4 × 45. × .8	662.4	
		Add one eighth of above for four days missing record in which the temperature did not rise above 75° F.	169.3	
	75–80	4.4 × 70. × .8	246.4	
	80–85	1.5 × 78. × .8	93.6	
	85–90	1.4 × 85. × .8	96.2	
		Total		1,959.5
April				
	40–65° F.	91.9 × 4.5 × .8	330.84	
	65–70	37.2 × 20. × .8	595.2	
	70–75	37.1 × 45. × .8	1,335.6	
	75–80	32.3 × 70. × .8	1,808.8	
	80–85	16.6 × 78. × .8	1,035.84	
	85–90	2.7 × 95. × .8	167.6	
		Total		5,273.88

The time at my disposal does not allow me to cite illustrations of the manner in which the results of the integration of the temperature given in these tables are correlated with distinctive formative and reproductive reactions in some of the species under critical observation in our experimental grounds. Some of these are notable and striking.

It need only be said in closing that not only may the exposures given above be evaluated in revised terms of growth of the wheat but they may also be converted into terms of growth or activity of any plant which has been the object of the necessary measurements.

Explanation of Plates XVII and XVIII.

Fig. 1. Graph showing relations of growth of wheat to temperature; compiled from data obtained by various authors and cited in Pfeffer's Plant Physiology, Eng. Ed.: 1903.

Fig. 2. Diagram of thermograph record of the Coastal Laboratory, Carmel, California, June 16–23, 1913, divided for measurement of areas to which growth values may be assigned.